An evaluation of species distribution models to estimate tree diversity at genus level in a heterogeneous urban-rural landscape

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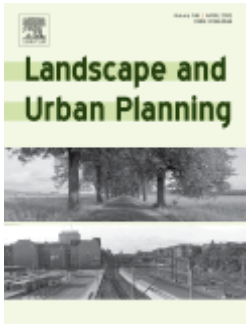

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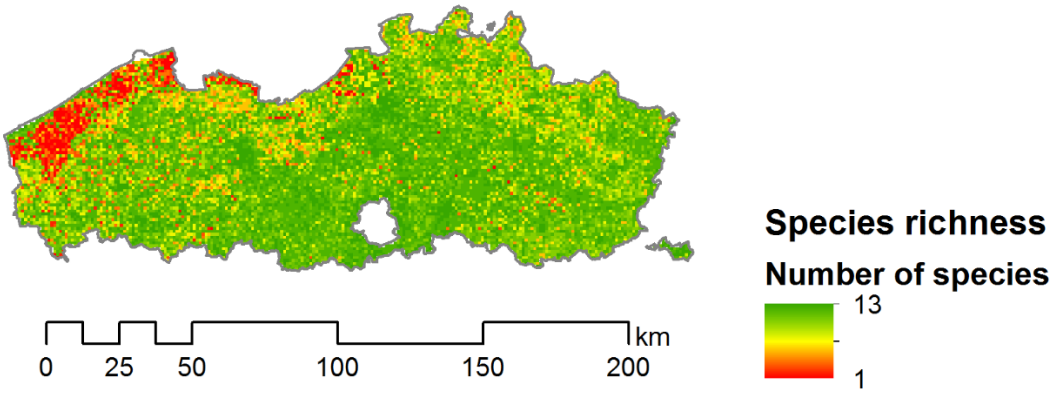

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Abstract

Trees provide ecosystem services that improve the environment and human health. The magnitude of these improvements may be related to tree diversity within green spaces, yet spatially explicit diversity data necessary to investigate such associations are often missing. Here, we evaluate two methods to model tree diversity at genus level based on environmental covariates and presence point data. We want to identify the drivers and suitable methods for urban and rural tree diversity models in the heterogeneous region of Flanders, Belgium.

We stratified our research area into dominantly rural and dominantly urban areas and developed distribution models for 13 tree genera for both strata as well as for the area as a whole. Occurrence data were obtained from an open-access presence-only database of validated observations of vascular plants. These occurrence data are combined with environmental covariates in MaxEnt models. Tree diversity is modelled by adding up the individual species distribution models.

Models in the dominantly rural areas are driven by soil characteristics (soil texture and drainage class). Models in the dominantly urban areas are driven by environmental covariates explaining urban heterogeneity. Nevertheless, the stratification into urban and rural did not contribute to a higher model quality. Generic tree diversity estimates were better when presences derived from distribution models were simply added up (binary stacking, True Positive Rate of 0.903). The application of macro-ecological constraints resulted in an underestimation of generic tree diversity (probability stacking, True Positive Rate of 0.533). We conclude that summing presences derived from species distribution models (binary stacking) is a suitable approach to increase knowledge on regional diversity.

HIGHLIGHTS:

- Rural species distribution models (SDMs) are driven by soil characteristics.
- Urban SDMs are driven by environmental covariates explaining urban heterogeneity.
- Summing presences derived from SDMs is suitable to assess diversity.
- Summing habitat suitability derived from SDMs underestimates diversity.

1. Introduction

Trees in urban environments deliver important ecosystem services. Street trees help to cool cities (Konarska *et al.*, 2016; Scholz *et al.*, 2018), partially mitigating the urban heat island effect and human heat stress (Lee *et al.*, 2016). Trees can also remove particulate matter from the atmosphere (Scholz *et al.*, 2018; Selmi *et al.*, 2016). Through climate regulation, air pollution mitigation and aesthetic and cultural values, trees contribute to better human well-being (Salmond *et al.*, 2016). Individual trees in the city also contribute to indirect nature experiences, which benefits human health (Cox *et al.*, 2019). The ecosystem services delivered by trees are tree species specific (Donovan *et al.*, 2005). Increasing biodiversity is expected to result in better ecosystem functioning and may yield more stable ecosystem services through time (Cardinale *et al.*, 2012).

Tree diversity has been studied at genus level before (Hoover et al., 2017; Hope et al., 2003) and might become more popular with increasing availability of observations from citizen science (Dobbs *et al.*, 2018). Observations of trees through citizen science initiatives have been found to be more accurate at genus level than at species level (Roman *et al.*, 2017). Plant genus-level diversity is strongly linked to plant species-level diversity (O'Brien *et al.*, 1998). Additionally, interactions with host plants often occur at genus level and therefore genus level diversity is also relevant for insect diversity (Kemp and Ellis, 2017), or ectomycorrhizal fungal diversity (Gao *et al.*, 2013). Thomsen *et al.* (2016) emphasize that a healthy urban tree population requires a high generic diversity. Modelling tree diversity at genus level is thus of high value because it encompasses more reliable observation data and allows for diverse applications.

Genus-level presence-only data can be used in species distribution models (SDMs). SDMs correlate species observations and environmental covariates to predict habitat suitability (Elith *et al.*, 2006). Applications of SDMs are manifold: identifying species distributions, studying

impact of climate and land use change scenarios (Dyderski *et al.*, 2018) and identifying areas of interest for conservation (McCune, 2016). Applications of SDMs in urbanized areas are not common (Della Rocca *et al.*, 2017), yet they have been successfully applied in urban green spaces (Milanovich *et al.*, 2012) and human-dominated landscapes (McCune, 2016).

Species richness can be modelled by stacking individual SDMs on top of one another to yield a total richness. Stacking of SDMs is most commonly done after thresholding the continuous probability output of the individual SDMs, a method known as binary stacking (Calabrese *et al.*, 2014). Nevertheless, discretizing continuous probabilities using fixed thresholds (for example considering all cases with a modelled probability of $p > 0.55$ as being present) is generally discouraged (Merow *et al.*, 2013). Instead, species-specific threshold rules can be applied (Cao *et al.*, 2013). Still, the literature suggests that binary stacking tends to overestimate species richness because biotic limitations are not accounted for (Calabrese *et al.*, 2014; Gavish *et al.*, 2017; Guisan and Rahbek, 2011). Nonetheless, combining binary SDMs is the most straightforward method to create species richness maps (Trotta-Moreu & Lobo, 2010). Combining continuous probability data, which is called probability stacking, is an alternative stacking approach (Calabrese *et al.*, 2014), although interpretations are less straightforward. Guisan & Rahbek (2011) have proposed a framework for spatially explicit species assemblage modelling (SESAM). In the SESAM framework, a macro-ecological model limits the number of species that can co-occur in one cell. One way of defining the macro-ecological constraint is by stacking the probabilities of SDMs (probability stacking). D'Amen *et al.* (2015) reduced overestimation by applying probability stacking successfully in the Alps of western Switzerland at a fine spatial resolution.

In this study, we test a stratified approach, in which we run separate SDMs for rural and urban areas in a mosaic landscape, to model tree diversity at genus level. We evaluate which environmental covariates drive the urban and rural models. First, we hypothesize that different

environmental covariates drive the urban and rural models. We expect that soil nutrients and soil moisture determine vegetation in rural areas, because this vegetation resembles the potential natural vegetation more closely (Walthert and Meier, 2017). For urban areas we expect an anthropogenic influence on the vegetation composition (Bourne and Conway, 2014). Second, we hypothesize that the application of a macro-ecological constraint to take biotic interactions into account would improve models for rural areas, but not for urban areas. We expect that biotic interactions are more relevant in rural areas (D'Amen et al., 2015). Third, we hypothesize that binary stacking performs sufficiently well in urban areas. We expect that biotic interactions are less relevant in urban areas because of human intervention.

2. Materials and methods

2.1. Study area and stratification

Flanders is the northernmost of the three administrative regions of Belgium with an area of 13,522 km^2 and a population density of 482 inhabitants per km^2. The area has a north-south soil gradient of decreasing fraction of sand and increasing fraction of silt. The climate according to Köppen is a maritime temperate climate (Cfb) (Peel *et al.*, 2007). The Organization for Economic Co-operation and Development (OECD) considers Flanders entirely as urbanized (Vervoort, 2016). Nevertheless, based on the Urban Audit of 2018 published by Eurostat, core cities and functional urban areas (FUAs) are delineated for Flanders. The delineation is used to distinguish dominantly urban areas from more rural areas in Flanders (Fig. 1). FUAs define a metropolitan area outside the geographical city boundaries, taking into account demographic, economic and environmental factors (Khalili *et al.*, 2018). In Flanders, the FUAs are located around the capitals of each province, except for Hasselt (Fig. 1). Hasselt is a provincial capital located in the east of the region where forest cover is higher. As only 10.6% of the study area consists of forest (De Keersmaeker *et al.*, 2015), other (urban)

green spaces are of high importance for biodiversity (Aronson et al., 2017; Lepczyk et al., 2017). Green space is most commonly defined as a vegetated area (Taylor and Hochuli, 2017). We will focus on vegetated areas containing woody vegetation. The Belgian and Luxemburg Institute for Floristics (IFBL) developed a regular grid of 4×4 km squares further divided into 1×1 km squares covering Belgium and Luxemburg. This grid is used as a reference for mapping species distributions (Van Rompaey, 1943). In this study the 1×1 km IFBL grid is used to mask observation data and environmental covariates.

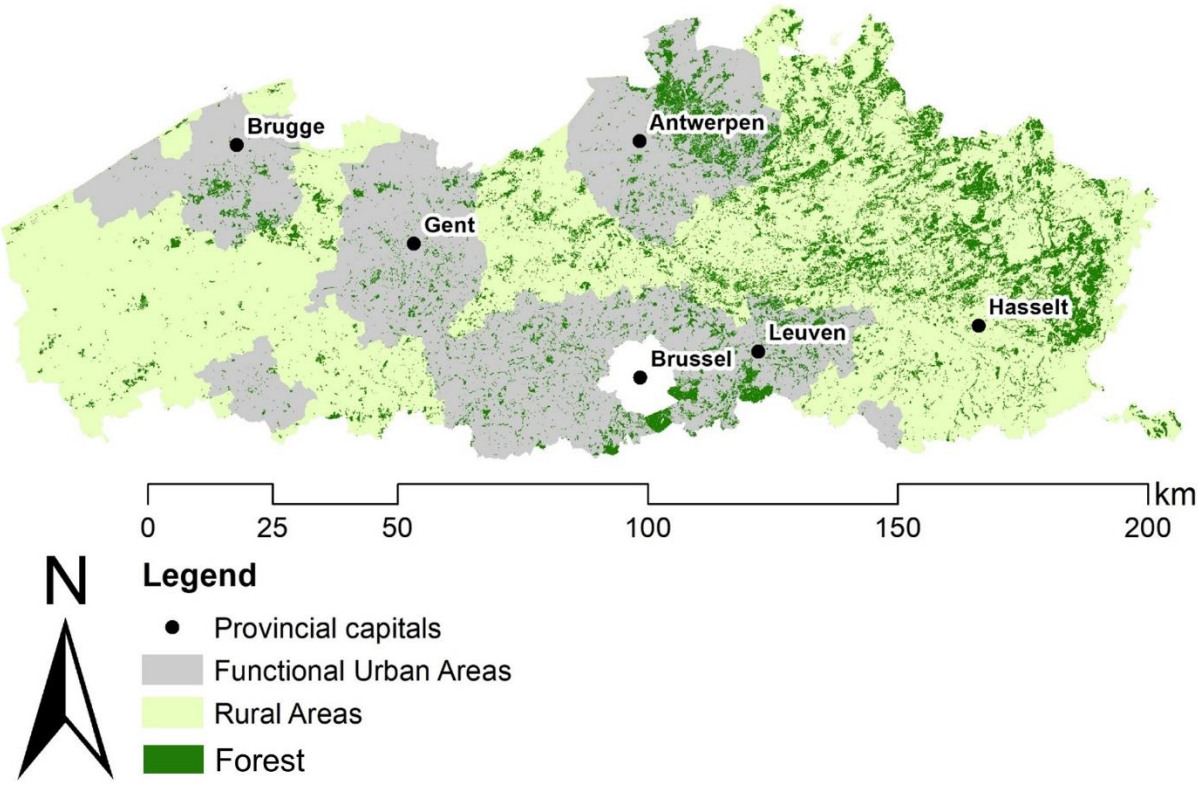

Fig. 1: Stratification of the Region of Flanders into functional urban areas and rural areas according to the Urban Audit of Eurostat (2018). The provincial capital cities are labeled and the forest cover in the region is visualized.

2.2. Species distribution modelling

Species distribution models (SDMs) estimate the relationship between recorded occurrences at sites (samples) and the environmental and/or spatial characteristics of those sites (environmental covariates) (Elith *et al.*, 2011). This relationship is then used to predict occurrences elsewhere. In the stratified approach, separate SDMs are run for the urban and rural strata. Subsequently, the urban and rural data are combined in an integrated approach to

form a model that covers the whole region of Flanders. The models are validated with independent field data to evaluate their utility in the urban and rural strata. The workflow for the integrated approach, which is parallel for the stratified approach, is visualized in Fig. 2 and explained in the following sections.

2.2.1. Occurrence data

The occurrence data of thirteen tree genera were included in the study: *Aesculus* (horse chestnut), *Alnus* (alder), *Betula* (birch), *Carpinus* (hornbeam), *Corylus* (hazel), *Fagus* (beech), *Fraxinus* (ash), *Juglans* (walnut), *Platanus* (plane), *Populus* (poplar), *Quercus* (oak), *Salix* (willow) and *Tilia* (linden). Presence-records of these genera were extracted from Florabank1 (Van Landuyt & Brosens, 2017) available on GBIF.org. The Florabank is an open-access presence-only database of validated observations of vascular plants, from checklists, literature and herbarium specimen information. The observations are georeferenced and attributed to the centers of 14317 1km×1km IFBL grid cells (Van Landuyt *et al.*, 2012).

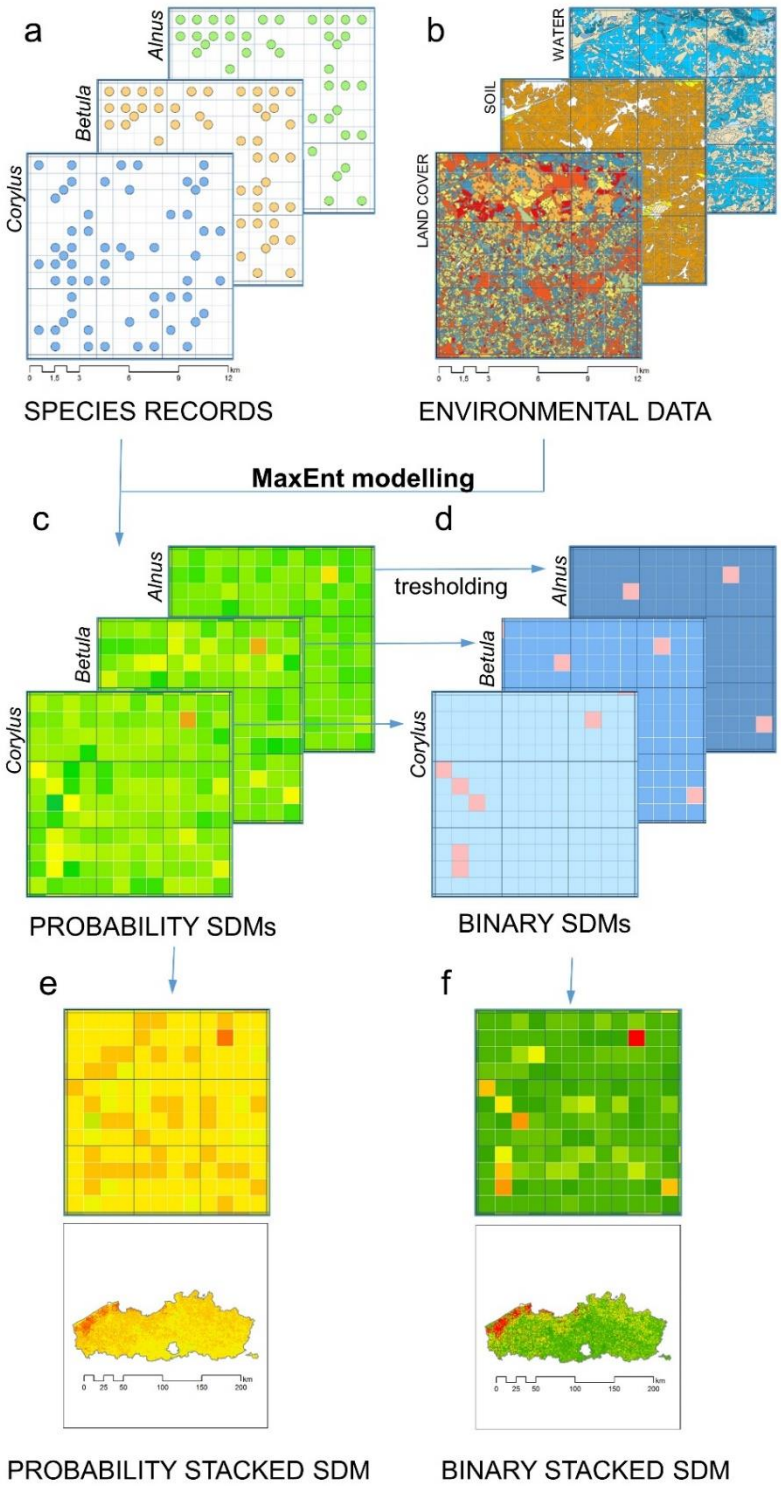

Fig. 2: Mapping tree diversity at the genus level from presence-only and environmental data. Presence-only data from Florabank (a) and environmental data from various sources (b) are combined in a Species Distribution Model (SDM) using MaxEnt. The continuous output of MaxEnt, probability models (c), can be converted to presence-absence models (binary SDMs) by applying genus specific thresholds (d). Stacking the probability models and applying the probability ranking rule results in a probability stacked SDM (e). Aggregating the thresholded SDMs results in a binary stacked SDM (f).

164 *2.2.2. Environmental covariates*

165 Soil texture class, soil drainage class, mean lowest and highest groundwater table depth, land
166 cover type and habitat type were the environmental covariates used. In Belgium, natural plant
167 communities are primarily determined by variation in soil nutrient content and soil moisture
168 (Cornelis *et al.*, 2009). Thus, soil texture and drainage class were extracted as categorical soil
169 variables from the Belgian soil map (Dondeyne *et al.*, 2014). This vector geodataset was first
170 resampled to a raster, using the IFBL grid as the mask layer and the cell assignment type
171 'maximum combined area'. The 'maximum combined area' rule selects the attribute value from
172 the polygon with the largest total area overlapping with the grid cell (ESRI, 2017). Mean
173 highest and lowest groundwater tables data were obtained from a soil hydrology raster
174 (ECOPLAN, 2014) and resampled to the IFBL grid.

175 Land cover data were obtained from one of the base layers in the ECOPLAN ecosystem
176 services information system (ECOPLAN, 2014). The geodataset contains a basic land cover
177 classification (the list of classes is available in Appendix 1). The grid with a spatial resolution
178 of 5m was resampled to the IFBL grid, retaining the land cover with the largest area in the grid
179 cell.

180 Habitat data were obtained from the Biological Valuation Map (BVM), a geodataset of habitat
181 types with attribute information on the ecological context and value of the delineated areas
182 (Vriens *et al.*, 2011). The BVM contains information about heterogeneity of urban areas, such
183 as the density and context of built-up areas, industrial areas and recreational areas. The classes
184 of the BVM are listed in Appendix 1. The BVM is a vector geodataset and was resampled to
185 the IFBL grid using 'maximum combined area' as the cell assignment type. Resampling and
186 masking of the environmental geodatasets were performed in ArcGIS 10.5.1-software (ESRI,
187 Redlands, CA, 2017).

188 *2.2.3. Probability models*

Probability models of the spatial distribution of each of the 13 genera were developed using MaxEnt version 3.3.3k. MaxEnt is a machine-learning algorithm highly suitable to develop models from presence-only data (Elith *et al.*, 2006; Phillips *et al.*, 2006). The algorithm is based on the principles of maximum entropy and finds an optimal probability distribution using a combination of occurrence data and environmental data (Elith *et al.*, 2011). MaxEnt is known to perform well even when environmental covariates are linearly correlated (De Marco and Nóbrega, 2018). The logistic output of MaxEnt is an attempt at expressing the raw output as a probability of presence (Elith *et al.*, 2011). A 10-fold cross validation was applied. Model performance was assessed with the area under the receiver operating characteristic curve (AUC) statistic, ranging between 0 and 1. When AUC values are higher than 0.5, the model performs better than a random distribution. For every genus, three models were developed: one using the entire dataset (integrated approach), then one for the rural and one for the urban areas (stratified approach). To evaluate the driving factors in these models, we determined the environmental covariate with the highest percentage of contribution to the model.

2.2.4. Binary stacking

We applied the '10 percentile training presence' rule on the MaxEnt-output (Ficetola *et al.*, 2009; Pearson *et al.*, 2006; Skowronek *et al.*, 2017), for every genus and model approach separately, resulting in a threshold value above which 90% of the training samples are correctly classified. Thus, a unique threshold value is used for every genus to create a binary output (0 = absence, 1 = presence). Binary stacking is the process of adding up the individual binary models, resulting in a generic tree diversity varying from 0 to 13 genera.

2.2.5. Probability stacking

As a cell-specific macro-ecological constraint we summed the MaxEnt-probabilities per grid cell (D'Amen *et al.*, 2015), resulting in a possible generic tree diversity range between 1.96 and 8.76. To determine which genera occur in the constrained cells we used the 'probability ranking' rule. The genera are assigned to the cell according to decreasing order of probability of presence determined from the SDMs (2.2.3), until the cell-specific macro-ecological constraint is reached. Probability ranking as described in the SESAM framework is incorporated in the package 'ecospat' available for R (Di Cola *et al.*, 2017) and was executed with R software 3.4.3 (R Core Team, 2017).

2.3. Validation

The probability models (2.2.3) were cross-validated before they were stacked. In addition, the stacked models were validated with independent field data. The independent field data consisted of recordings of the genus's occurrence around 208 randomly selected point locations, with a search effort per point of ten minutes with two observers. The sampling protocol is derived from the timed-meander sampling protocol (Goff *et al.*, 1982), which is applied in various fields of ecology (Threlfall *et al.*, 2017) and is favored because of its cost-effectiveness (Hamm, 2013). The 208 point locations are distributed over 130 IFBL cells. There are 87 rural cells and 43 urban cells. A genus is present in a cell if it is observed in at least one of the random point locations within the cell. The field data are assumed to provide the true condition that is compared to the predicted condition provided by the SDMs at genus level. True condition data and predicted condition data were compared in a confusion matrix, describing true positive (TP), true negative (TN), false positive (FP) and false negative (FN) outcomes. Based on the values in the confusion matrix, we evaluated the model performance by calculating the true positive rate (TPR). TPR is the number of true positives divided by the total of positive cases, the sum of true and false positives. The TPR informs simultaneously

about the presences that are correctly predicted and about those that were incorrectly identified as positives. A TPR of 80% would indicate that 80% of the presences are true positives while 20% are false positives. However, in the present study, the false positives are not necessarily false as the species could have been missed during the validation field work. Therefore we focus on the true positives when interpreting the TPR. Additionally, the percentage of false negatives is included in the evaluation, because this percentage provides information on the underestimation of the stacking method. The higher the percentage of false negatives, the more the tree diversity at genus level is underestimated.

2.4 Compare model outcomes

To compare model outcomes we calculated average modelled tree diversity at genus level and 95% confidence intervals for binary stacked vs. probability stacked models and for integrated vs. stratified approaches and for urban vs. rural areas. We used the paired sample t-test (with a statistical cutoff value of 0.05) to test whether overall average modelled tree diversity at genus level differed between binary stacked and probability stacked models. We then used the paired sample t-test to test whether modelled generic tree diversity differed between integrated and stratified approaches within the binary stacked models, both for the entire dataset and for a dataset stratified in urban vs. rural areas.

3. Results

3.1 Probability models

The species distribution models outperformed the random spatial distribution (all AUC > 0.5; Table 1), for the stratified approach as well as the integrated approach. On average the AUC is 0.60 with a standard deviation of 0.007. The strength of the strongest predictor ranges from 32.7-85.7 percent of contribution (Table 1). For 11 out of 13 urban models, the strongest predictor is the Biological Valuation Map (BVM), containing information on urban heterogeneity. For the rural model as well as the integrated model, we found that for some genera the strongest predictors were the soil variables texture class and drainage class.

Table 1: Summary of the species distribution models for each genus. Reporting the number of grid cells occupied by an observation (presences), the average area under the curve (AUC) as a measure to evaluate the models, the standard deviation of the AUC (SD), the strongest predictor (SP) and the percent of contribution (PC) of this strongest predictor to the MaxEnt model. (BVM = Biological Valuation Map)

		Rural stratum				Urban stratum				Integrated model			
Genus	**presences**	**AUC**	**SD**	**SP**	**PC**	**AUC**	**SD**	**SP**	**PC**	**AUC**	**SD**	**SP**	**PC**
Aesculus	1162	0.63	0.03	BVM	54.3	0.62	0.04	BVM	61.2	0.64	0.03	BVM	55.1
Alnus	6918	0.55	0.01	BVM	38.0	0.54	0.02	BVM	40.7	0.54	0.01	BVM	39.9
Betula	8888	0.60	0.01	BVM	40.9	0.58	0.02	BVM	45.6	0.58	0.01	BVM	47.7
Carpinus	3029	0.64	0.02	texture class	42	0.63	0.02	BVM	29.2	0.63	0.02	texture class	41.3
Corylus	5490	0.60	0.02	texture class	45.8	0.59	0.02	BVM	34.5	0.59	0.01	texture class	47.1
Fagus	2710	0.64	0.02	drainage class	38.1	0.64	0.02	BVM	32.7	0.64	0.02	drainage class	37.2
Fraxinus	6635	0.58	0.01	texture class	67.6	0.55	0.02	texture class	42.6	0.57	0.01	texture class	71.2
Juglans	1833	0.61	0.03	texture class	44.9	0.59	0.03	BVM	40.3	0.61	0.02	texture class	46.5
Platanus	50	0.63	0.34	BVM	47.5	0.90	0.06	BVM	81.7	0.81	0.10	BVM	85.9
Populus	5380	0.57	0.02	drainage class	55.9	0.56	0.02	BVM	41.8	0.56	0.01	drainage class	47.1
Quercus	8182	0.57	0.01	BVM	36.2	0.55	0.02	texture class	38.4	0.55	0.01	BVM	38.7
Salix	8349	0.53	0.01	drainage class	65.0	0.52	0.02	BVM	39.9	0.52	0.01	drainage class	46.4
Tilia	1171	0.61	0.04	BVM	42.6	0.63	0.04	BVM	54.3	0.64	0.03	BVM	43.8

3.2 Stacked species distribution models

For the integrated as well as the stratified approach binary stacking resulted in a generic tree diversity varying between 0 and 13. Probability stacking resulted in a lower generic tree diversity between 2 and 9 (Fig. 3). Spatial differences in generic tree diversity between the integrated and the stratified approach are not strongly pronounced.

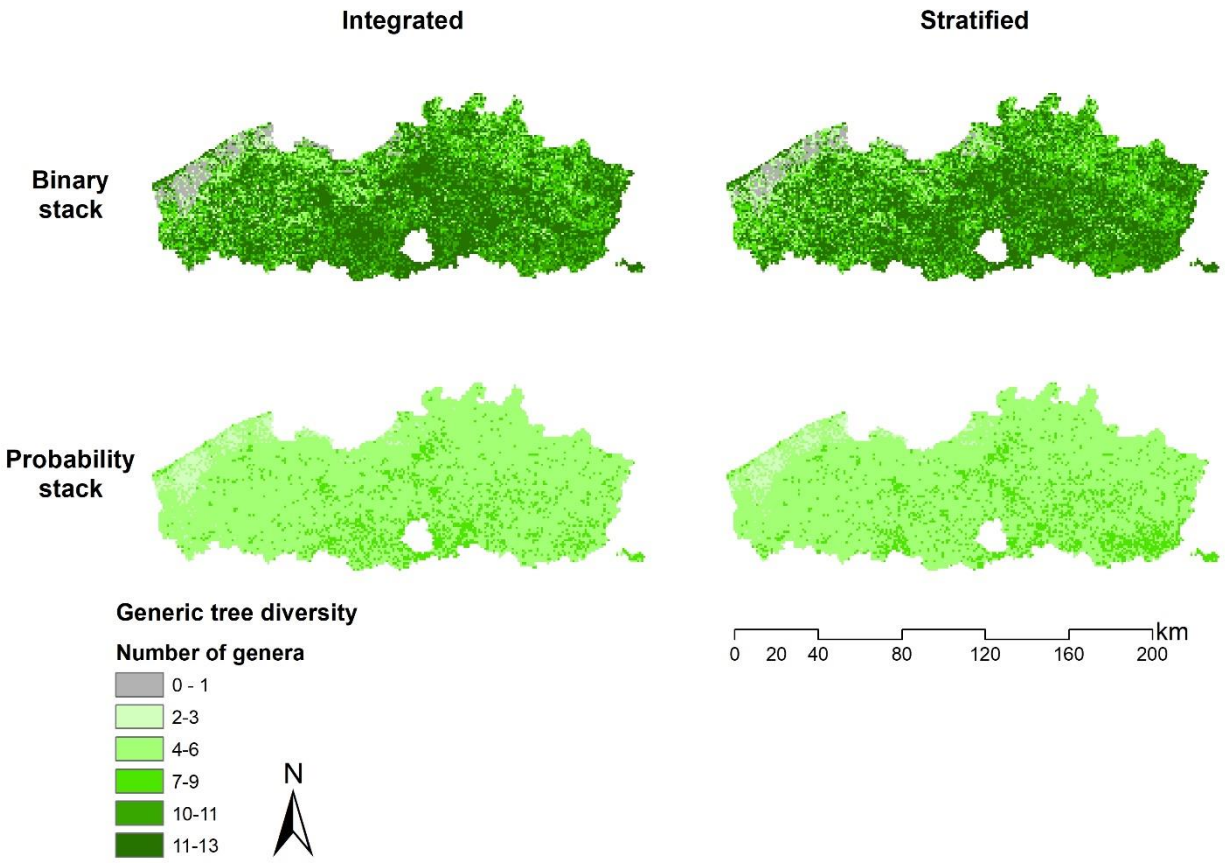

Fig. 3: Tree diversity at genus level determined by binary (upper) and probability (lower) stacking of the MaxEnt models developed in an integrated (left) and stratified (right) modelling approach. The cell size is 1km×1km.

3.3 Validation

The binary stacking method, with an overall TPR of 0.90, performed better than the probability stacking method, with a considerably lower overall TPR of 0.52-0.53 (Table 2). Overall, the integrated and the stratified approach performed equally well. The binary stacking method had a lower percentage of false negatives (6.0 - 6.1 %) than the probability stacking method (29.3 – 29.9 %) (Table 3).

Table 2: Validation results: true positive rate (TPR) derived from the confusion matrix.

		TPR		
Model	Approach	Overall	Urban	Rural
Binary stacked	Integrated	0.90	0.94	0.89
	Stratified	0.90	0.95	0.88
Probability stacked	Integrated	0.53	0.54	0.53
	Stratified	0.52	0.53	0.53

Table 3: Validation results: percentage of false negatives (%) derived from the confusion matrix.

		FN (%)		
Model	Approach	Overall	Urban	Rural
Binary stacked	Integrated	6.1	4.3	7.0
	Stratified	6.0	3.3	7.3
Probability stacked	Integrated	29.3	30.8	28.6
	Stratified	29.9	31.5	29.2

3.4 Comparison of model outcomes

3.4.1 Binary stacking vs. probability stacking

The overall average tree diversity at genus level was higher for binary stacked models (9.8-9.9) than for probability stacked models (5.6) (Table 4). The diversity based on the validation data was 8.1, in line with results from the binary stacking approach. There was a significant mean difference of 4.3 (95% CI 4.2-4.3) between binary stacked and probability stacked models for the integrated approach (paired t-test $t = 200.1$, $df = 13458$, $p < 0.001$). There was a significant mean difference of 4.2 (95% CI 4.1-4.3) between binary and probability stacked models for the stratified approach (paired t-test $t = 153.7$, $df = 13458$, $p < 0.001$).

Table 4: Average modelled tree diversity at genus level based on binary and probability stacked models, for integrated and stratified approaches and for urban and rural areas.

		Tree diversity (95% CI)		
Model	Approach	Overall	Urban	Rural
Binary stacked	Integrated	9.9 (9.8-9.9)	10.1 (10.0-10.1)	9.8 (9.7-9.8)
	Stratified	9.8 (9.7-9.8)	9.5 (9.4-9.6)	10.0 (9.9-10.0)
Probability stacked	Integrated	5.6 (5.6-5.6)	5.7 (5.7-5.8)	5.6 (5.5-5.6)
	Stratified	5.6 (5.6-5.6)	5.5 (5.5-5.6)	5.6 (5.6-5.6)
Validation data		8.1 (7.6-8.7)	8.6 (7.8-9.5)	7.9 (7.3-8.6)

3.4.2 Binary stacking: rural vs. urban areas

For binary stacked models, the integrated approach yielded a statistically significant higher overall estimated tree diversity at genus level [mean difference integrated vs. stratified 0.09 (95% CI 0.06-0.11), $t = 6.72$, $df = 13458$, $p<0.001$]. However, subtracting the stratified result from the integrated result revealed a spatial differentiation (Fig. 4). The stratified approach resulted in a significantly higher diversity in the rural areas, thus a negative mean difference of –0.18 (95% CI -0.21 – -0.15) ($t = -12.5$, $df = 8359$, $p<0.001$). The integrated approach, however, resulted in a significantly higher diversity in the urban areas, thus a positive mean difference of 0.52 (95% CI 0.48-0.57) ($t = 22.3$, $df = 5098$, $p<0.001$).

Green pixels (Fig. 4) represent a higher diversity obtained with the integrated approach. These green pixels are often clustered within the FUAs (black outline, Fig. 4). Conversely, red pixels represent a higher diversity obtained with the stratified approach. These red pixels are observed in clusters outside the FUAs, especially in extremely rural areas such as: 'De Westhoek' in the west and 'Haspengouw' in the south-east of Flanders (Fig. 4).

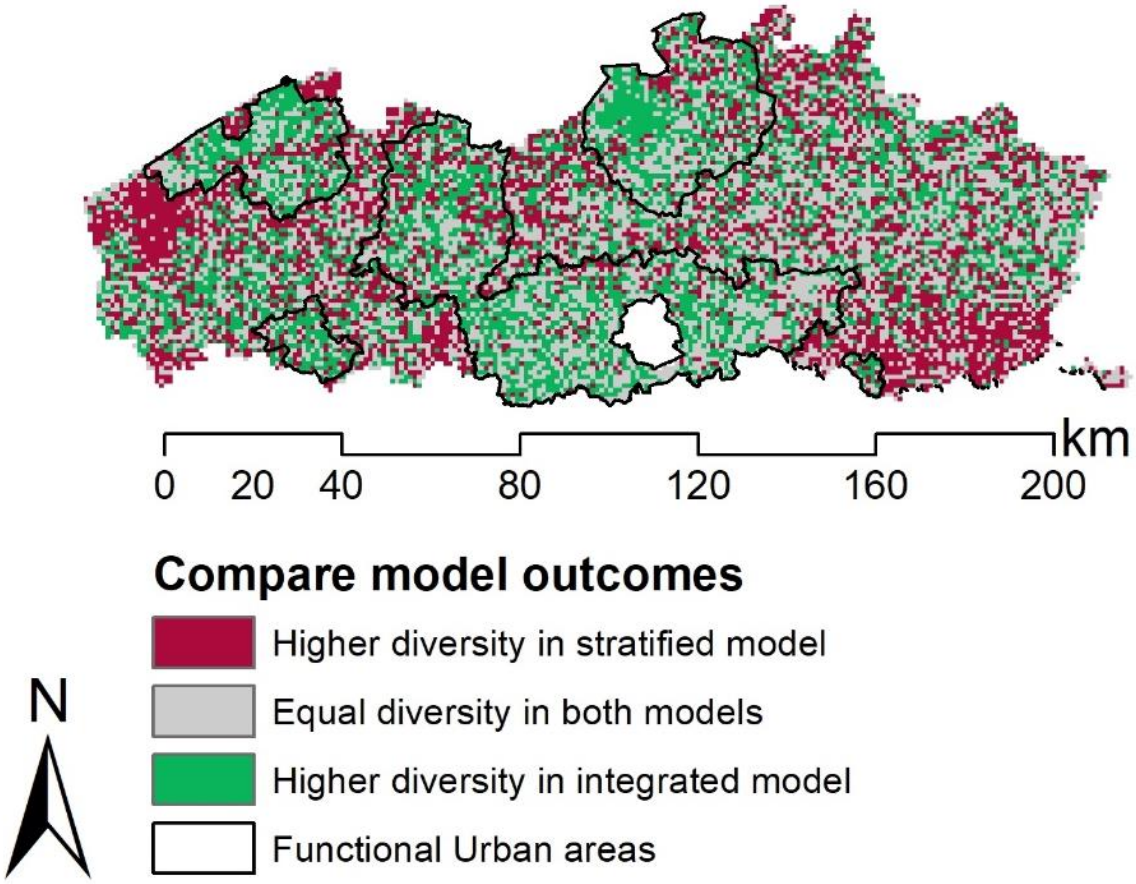

Fig. 4: The difference in the binary stacking results from the integrated and stratified approach. Cell size is 1km×1km.

4. Discussion and conclusions

4.1 Environmental covariates

Rural and urban models were driven by different environmental covariates, which confirms the first hypothesis. As expected, soil variables, such as texture class and drainage class, were of high importance to explain the distribution of native trees in rural areas. Texture class was an important covariate for *Corylus*, for example, because this genus requires richer loamy soils (Özenç, 2001). *Salix* and *Populus* can tolerate wet soils (Zalesny and Bauer, 2007) and as a result drainage class was an important environmental covariate in their SDMs. Earlier studies demonstrated that including soil factors in plant SDMs results in improved predictions (Buri *et al.*, 2017). For urban areas we expected that the vegetation would be determined by anthropogenic influences. The urban heterogeneity, which is better described in the Biological Valuation Map (BVM), was the most important covariate in the urban SDMs (Table 1). In the BVM seven urban/built up types are included (ua, ud, un, ur, uv, uc and ui), while the the other land cover map (ECOPLAN) contains only three urban land cover types (9101, 9201, 9202) (see Appendix 1). It has been emphasized in the past that including environmental covariates that account for the diverse functions of urban areas is important to understand urban plant species patterns (Godefroid and Koedam, 2007). Future developments of species distribution models in urban areas need to include covariates that address the variety of anthropogenic influence.

4.2 Stacking methods

At a fine spatial resolution, as in the work of D'Amen *et al.* (2015), binary stacking overestimates species diversity in a natural environment, because dispersal limitations and biotic interactions are not taken into account. In this study, however, we worked at a spatial resolution of 1km×1km and biotic interactions are less important at this relatively coarse resolution (Thuiller *et al.*, 2015). The probability stacking method should prevent from overestimating tree diversity at genus level. Nevertheless, the low true positive rate (Table 2)

and the high percentage of false negatives (Table 3) showed that the probability stacking method underestimated tree diversity in Flanders. Additionally, in urbanized areas, human decision-making and management most likely override natural species selection and biotic interactions are therefore less likely to drive species composition. Therefore, binary stacking is the preferred method for biodiversity modelling at 1km×1km resolution in both urban areas and rural areas. Nevertheless, the scale-dependent applicability of a macro-ecological constraint needs further research as there is, to our knowledge, no literature on this topic.

4.3 Comparison of model outcomes

Binary stacking resulted in a significantly higher diversity at genus level compared to probability stacking (Table 4). This difference is not an overestimation of binary stacking, but due to an underestimation of probability stacking. Using the binary stacking method and the stratified approach, higher diversity was clustered in the rural areas (Table 4 and Fig. 4). Rural areas are thus more prone to overestimation and would probably benefit more from applying macro-ecological constraints, compared to urban areas. Nevertheless, applications of macro-ecological constraints seem to be of higher relevance in more natural areas (D'Amen *et al*., 2015), far less urbanized than the rural areas in Flanders.

To conclude, we find that binary stacking is most suitable for both urban and rural areas in Flanders. Stratification of the study area did not improve model quality considerably, but confirmed that different environmental covariates contributed to the models of urban and rural areas. Probability stacking is to be considered in natural areas, but does not perform well in urbanized areas, especially at the moderate spatial resolution of 1km×1km.

4.4 Limitations

All Species Distribution Models (SDMs) had relatively low Area Under the Curve values (average AUC: 0.60± 0.01), but all performed better than random distributions (Table 1). By

stacking SDMs, errors in individual species models accumulate and degrade predictions of species diversity (D'Amen *et al.*, 2015; Pottier *et al.*, 2013). The importance of the BVM as an environmental covariate emphasizes the relevance of including urban heterogeneity in SDMs. Unfortunately, at a moderate resolution of 1×1km relevant intra-urban variation of the tree canopy (Weinberger *et al*., 2016) cannot be observed.

4.5 Applications

The model resulting from this study can be expanded by stacking more binary SDMs, by producing species-level models or by producing models of other plant groups. Spatially-explicit biodiversity data are vital for emerging environmental health studies (McInnes *et al.*, 2017), for example to study relationships between residential and dynamic exposure and human health outcomes (Cox *et al.*, 2017; Shanahan *et al.*, 2016). Hjort et al. (2016) present a concept to calculate individual long-term or life time exposure to pollen with geographic information systems. Landscape and urban planners could also use tree diversity maps to identify areas with low diversity and optimize the delivery of ecosystem services or decrease potential social inequalities in access to biodiverse green space by increasing biodiversity in focus areas (Wolch *et al*., 2014). Finally, when subsets of models for allergenic species are used, diversity maps could be interpreted as allergy risk maps and inform pollen allergy patients about pollen allergy risks (McInnes *et al*., 2017).

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Appendix 1:

Table 1: Ecoplan land cover classification (in Dutch). Retrieved from: https://www.uantwerpen.be/nl/onderzoeksgroep/ecoplan/ecoplan-tools/ecoplan-geoloket/

Complex	**Code**	**Dutch name**
water	10101	Stilstaand water
	10201	Getijde mesohaline
	10202	Getijde Oligohalien
	10203	Getijde zoet
	10204	Zoet
	10301	Zee
Bush land	1101	Ruigten en pioniersvegetatie
	1201	Struweel
	1301	Struiken boomgaard
	1302	Laagstam
	1303	Hoogstam
	1401	Ander hooggroen
	1402	Ander laaggroen
Forest complexes	2101	Berk
	2102	Beuk
	2103	Beuk – naaldhout
	2104	Eik
	2105	Eik – naaldhout
	2106	Populier
	2107	Populier – naaldhout
	2108	Ander loofhout
	2109	Ander loofhout – naaldhout
	2201	lork
	2202	Lork – loofhout
	2203	Fijnspar
	2204	Fijnspar – loofhout
	2205	Zwarte den
	2206	Zwarte den – loofhout
	2207	Grove den
	2208	Grove den – loofhout
	2209	Ander naaldhout
	2210	Ander naaldhout – loofhout
Grasslands	3101	Voedselarm grassland
	3102	Voedselrijk grassland
	3201	Voedselrijk grasland
Heath lands	4101	Droge heide
	4201	Vochtige heide
Bare soils	5101	Kale bodem
	5201	Duinen
	5301	Strand
	5401	Niet verharde wegen
Agricultural land	6101	Aardappel
	6102	Mais
	6103	Graan
	6104	Zaden
	6105	Peulvruchten
	6106	Suikerbiet

	6107	Groenten
	6108	Kruiden
	6109	Fruit
	6110	Vlas en hennep
	6111	Voedergewassen
	6112	Andere akker
	6201	Eénjarige sierplanten
	6202	Meerjarige sierplanten
	6203	Kerstbomen
Wet vegetation types	7101	Moeras
	7201	Rietland
	7301	Alluvial bos
	8101	Slikken
	8201	Schorren
Built up area	9101	Gebouwen
	9201	Verhard
	9202	Verhard andere

Table 2: Biological valuation map classification of habitat types (in Dutch). Retreived from: https://www.geopunt.be/catalogus/datasetfolder/bf31d5c7-e97d-4f71-a453-5584371e7559

Complex	**Code(s)**	**Dutch name**
Stagnant water	ad	Bezinkingsbekken
	ae, aer, aev	Eutroof
	ap, apo, app	Diep of zeer diep water
	ao, aoo, aom	Oligotroof tot mesotroof water
	ah	Brak of zilt water
Swamps	ms	Zuur laagveen
	mm	Galigaanvegetatie
	mk	Alkalisch laagveen
	mc	Grote zeggenvegetatie
	mz	Brak tot zilt moeras
	mr	Rietland en andere Phragmition vegetaties
	md	Drijfzoom en/of drijftil
Grasslands	ha	Struisgrasvegetatie
	hc	Dotterbloemgrasland
	hk	Kalkgrasland
	hm, hmm, hme	Vochtig schraalgrasland
	hmo	Vochtig heischraalgrasland
	hn	Droog heischraalgrasland
	hu	Mesofiel hooiland
	hj	Vochtig grasland gedomineerd door russen
	hp×, hpr×	Soortenrijk premanent cultuurgrasland
	hpr(×)+da, hp(×)+da, h+da	Soortenrijk premanent cultuurgraslandmet zilte elementen
	hp	Soortenarm permanent cultuurgrasland
	hx	Zeer soortenarm, vaak tijdelijk grasland
	hf, hfc, hft	Moerasspirearuigte
	hr	verruigd grasland
	hz	grasland op zware metalen vergiftiged bodems
	hpr	weidelandcomplex met veel sloten of microreliëf

High fenn	t	hoogveen
Heath lands	cg	Droge struikheivegetatie
	cv	Droge heide met bosbes
	ce, ces	Vochtige tot natte dopheivegetatie
	cm	Gedegradeerde heide met dominantie van pijpenstrootje
	cp	Gedegradeerde heide met dominantie van adelaarsvaren
	cd	Gedegradeerde heide met dominantie van bochtige smele
Dunes and tidal flats	ds	Slikken
	da	Schorre
	dd	Stuifduinen aan de kust
	dl	Strand
	dz	Zandbank
Bush land	sd(b)	Duinstruweel
	sp	Doornstruweel
	sk	Struweel op kalkrijke bodem
	sg, sgu, sgb	Brem- en gaspeldoornstruweel
	sz	Opslag van allerlei aard
	sf	Vochtig wilgenstruweel op voedselrijke bodem
	so	Vochtig wilgenstruweel op venige of zure grond
	sm	Gagelstruweel
	se	Kapvlakte
Beech forests	fe	Beukenbos met wilde hyacint
	fa	Beukenbos met voorjaarsflora, zonder wilde hyacint
	fm	Beukenbos met parelgras en lievevrouwebedstro
	fk	Beukenbos op mergel
	fl	Beukenbos met witte veldbies
	fs	Zuur beukenbos
Oak forests	qe	Eiken-haagbeukenbos met wilde hyacint
	qa	Eiken-haagbeukenbos
	qk	Eiken-haagbeukenbos op mergel
	ql	Eikenbos met witte veldbies
	qs	Zuur eikenbos
	qb	Eikenberkenbos
Wet forests	vc	Bronbos
	va	Alluviaal elzen-essenbos
	vf	Elzen-eikenbos
	vn	Nitrofiel alluviaal elzenbos
	vm	Elzenbroek
	vo	Oligotroof elzenbroek met veenmossen
	vt	Berkenbroek
Ruderal forests	ru, rud	ruderaal olmenbos
Coniferous forests	pi, ppi, pa, ppa	Naaldhoudsbestand zonder ondergroei
	pmh, pms, pmb, ppmh, ppms, ppmb	Naaldhoutbestand met ondergroei
Poplar forests	lhi, lhb, lsi, lsb, lsh	Populiersbestand

Other deciduous forests	n	Loofhout aanplant (exclusief populier)
Agricultural fields	bk, bl, bs, bu	Akker
Urban and built up areas	ua, ud, un, ur	Bebouwing
	uv, uc	Recreatiegebied
	ui	Industrie
Small landscape elements	kj	Hoogstamboomgaard
	kb	Bomenrij
	kh	Houtkant
	khw	Houtwal
	k	lijnvormige begroeiing van perceelsranden, sloten en bermen
	kk	Doline, ingang ondergrondse mergelgroeve
	km	Muurvegetatie
	kn	Veedrinkpoel
	kt	Talud
	kw	Holle weg
Other mapped elements	ko	Stort
	kr	Groeve
	kf	Voormalig militair fort
	kg	Terril
	kz	Opgehoogd terrein
	ki	Vliegveld
	kg	Kwekerij of Serre
	ka	Eendenkooi
	kr	Rots
	kd	Dijk
	ks	Verlaten spoorweg
	kl	Laagstamboomgaard
	kp	Park
	kpa	Arboretum
	kpk	Kasteelpark